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Dentition of Blenniid Fishes in the Subfamily Salariinae with Premaxillaries and Dentaries forming a Complete Shell (Pisces: Blenniidae)

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With 16 figures

Summary

The dentition of Group 4 of salariine blennies (species with the upper and lower jaws forming a complete shell) is examined in the present paper. The distance between the bases of the functional teeth and the jaw margins, and the density, localisation and configuration of the bony particles in the membrane connecting the bases of the functional teeth with the posterior margins of the jaw bones, are highly variable. These characters are described for *Alticus andersonii*, *Blenniella cyanostigma*, *Entomacrodus cadenati*, *E. vermiculatus*, *Exallias brevis*, *Istiblennius edentulus*, *Ophioblennius atlanticus*, *Praealticus tanegasimae*, *Salarias fasciatus*, and *S. sinuosus*.

The significance of the characters for the evolution of Group 4 is discussed. It seems evident that bony particles in Group 4 are faster reduced in the dentary membrane than in the premaxillary membrane. A reason may be the originally more stable situation of the dentary with its joint connection between articular and quadrate towards the viscerocranium. On the other hand, the premaxillary is attached to the maxillary, the palatine and to the median ethmoid (with the processus acscendens) by connective tissue only.

Zusammenfassung

Die Bezahnung in der Gruppe 4 der Schleimfische der Unterfamilie Salariinae (Arten mit Ober- und Unterkiefer in kompletter Schalenform) wird in der vorliegenden Arbeit untersucht. Besonders die Distanz zwischen den Basen der funktionellen Zähne und den Kieferrändern, die Dichte, Lokalisierung und Konfiguration der in die Verbindungsmembran zwischen den Basen der funktionellen Zähne und den posterioren Rändern der Kieferknochen eingelagerten Knochenteilchen weisen eine hohe Variabilität auf. Die Ausprägung dieser Merkmale wird für *Alticus andersonii*, *Blenniella cyanostigma*, *Entomacrodus cadenati*, *E. vermiculatus*, *Exallias brevis*, *Istiblennius edentulus*, *Ophioblennius atlanticus*, *Praealticus tanegasimae*, *Salarias fasciatus* und *S. sinuosus* beschrieben.

Die evolutionäre Bedeutung für die Entwicklung der Gruppe 4 wird untersucht. Bezüglich der Einlagerung von Knochenpartikeln in die Verbindungsmembranen zwischen Zähnen und Kieferknochen scheint es evident zu sein, dass die Knochenpartikel im Unterkiefer schneller

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als im Oberkiefer reduziert werden. Ein Grund hierfür scheinen die primär stabileren Verhältnisse des Unterkiefers zu sein (mit seiner Gelenkverbindung zwischen Articulare und Quadratum zum Viscerocranium), im Gegensatz zu den lediglich bindegewebigen Verbindungen von Praemaxillare mit Maxillare und Palatinum sowie des Processus ascendens mit dem Medianethmoid zu sein.

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1. Introduction

Blenniid fishes are a group of small benthic shorefishes living circumtropical in warm and temperate oceans. NORMAN (1943) was the first to publish an infrafamilial classification of the Blenniidae including a synopsis of blenniid fish genera. Species of the family Blenniidae were grouped in three subfamilies, mainly on the basis of different types of dentition: Ophioblenniinae, Blenniinae, and Salariinae.

Later authors modified NORMAN's classification into present usage. The main works were published by SPRINGER (1967, 1968, 1972, 1976, 1988), SMITH-VANIZ & SPRINGER (1971), SPRINGER & SMITH-VANIZ (1972), SMITH-VANIZ (1975, 1976), SPRINGER & GOMON (1975), BATH (1977, 1982, 1983, 1989, 1990, 1992, 1994, 1996, 2000a, 2000b, 2001), WILLIAMS (1988, 1990), BATH & WIRTZ (1989, 1992), and SPRINGER & WILLIAMS (1994). On the basis of osteological characters, SPRINGER (1968) distinguished within the family Blenniidae a subfamily Blenniinae with the three tribes Blenniini, Omobranchini and Salariini, and another subfamily Nemophidinae. SPRINGER & SMITH-VANIZ (1972) erected another tribe, Phenablenniini, represented by the monotypic genus *Phenablennius* Springer & Smith-Vaniz, with *Phenablennius heyligeri* as the only species. In the same paper (SPRINGER & SMITH-VANIZ, 1972: 64), the subfamily Nemophidinae was degraded into a tribe Nemophini without comment; it was later revised as tribe Nemophini by SMITH-VANIZ (1976). In the latter revision, SMITH-VANIZ made a detailed examination of the phylogenetic position of the Nemophini within the family Blenniidae; considering plesiomorphic and apomorphic characters, he recognised 6 major lineages within the family Blenniidae: Tribe Salariini; "Blenniini"-group; species of genus *Blennius*; Tribe Omobranchini; Tribe Phenablenniini; Tribe Nemophini.

BOCK & ZANDER (1986) included the genera of the "Blenniini"-group in a new tribe Parablenniini, which they proposed to be the sister-tribe of the Salariini. On the other hand, they recognised the tribes Blenniini (including species of the genus *Blennius*), Omobranchini, Phenablenniini, and Nemophini, thus adding to 6 tribes within the family Blenniidae.

WILLIAMS (1990) again examined the phylogeny of the tribes of blenniid fishes; he hypothesized a close relationship between the tribes Parablenniini. In a preliminary hypothesis of the blenniid tribe relationships, he divided the Salariini into two

groups, a *Rhabdoblennius*-group with an atypical dentition, and a *Salarias*-group with a typical dentition (WILLIAMS, 1990: fig. 1).

BATH (2001) raised the blenniid fish tribes to subfamilies according to ICZN rules; he examined various osteological and morphological characters of the subfamily Salariinae, and found that the Parablenniinae is a junior synonym of the Salariinae. Within the subfamily Salariinae, BATH (2001) distinguished 4 species-groups on the basis of different types of dentition: Group 1 (incisiform dentition), Group 2 (intermediate between incisiform and comblike), Group 3 (premaxillaries and dentaries forming an incomplete shell), Group 4 (premaxillaries and dentaries forming a complete shell). Species of Group 4 examined by BATH (2001) were defined as sharing the following characters: premaxillaries and dentaries forming a complete shell; connective tissue between functional teeth of the premaxillary and posterior-inferior premaxillary margin just like the dentary and posterior-superior margin, either with inlays or irregular bony fragments (in that case premaxillary and dentary margin without sharp contour), or without such inlays (then premaxillary and dentary margin with sharp contour).

Some of these characters are subject to significant variation; it therefore seemed necessary to examine and describe them again in detail. The distance between the bases of the functional teeth and the jaw margins, their density, the localisation and configuration of the bony inlays in the connective tissue membrane between the bases of the functional teeth and the posterior margins of the jaw bones of Group 4 are re-examined in the present paper.

2. Methods, materials, acknowledgement

2.1. Methods

Measurements were made with a mechanical dial caliper to the nearest 0.1 mm. Standard length (*SL*) was measured from the mid-tip of the upper lip to the distal end of the urostyle; total length (*TL*) was measured from the mid-tip of the upper lip to the tip of the longest caudal fin ray.

All specimens were treated with the trypsin-alizarin method of TAYLOR (1967). On the basis of cleared-and-stained specimens, additional preparations were made.

Photographs were taken with a ZEISS binocular SR, a photo tube and a LEICA R4 camera, using AGFAPAN AP x 25 films.

The osteological nomenclature follows SPRINGER (1968) and BATH (2001). The following abbreviations are used in the figure captions:

ACT Anterior canine tooth;
AID anterior-inferior margin of the dentary;
ASP anterior-superior margin of the premaxillary;
BP bony particle;
BR rodlet-like bony particle;
BRO rows of bony particles;
CTI connective tissue;
CTO canine tooth;
DE dentary;
ET dental enamel;
FT functional teeth;
PIP posterior-inferior margin of the premaxillary;
PM premaxillary;
PPS ascending process of premaxillary;
PSD posterior-superior margin of dentary;

RT replacement teeth;
TR tooth ridge.

2.2. Materials

For the osteological examination of premaxillaries and dentaries, the specimens listed below were examined (genera and species in alphabetical order; standard length is given in mm). The following acronyms are used in the text:
SB Sammlung BATH, Pirmasens, Germany;
SMNS Staatliches Museum für Naturkunde, Stuttgart, Germany;
USNM National Museum of Natural History, Smithsonian Institution, Washington D.C., U.S.A.

Material for osteological examination

Family Blenniidae

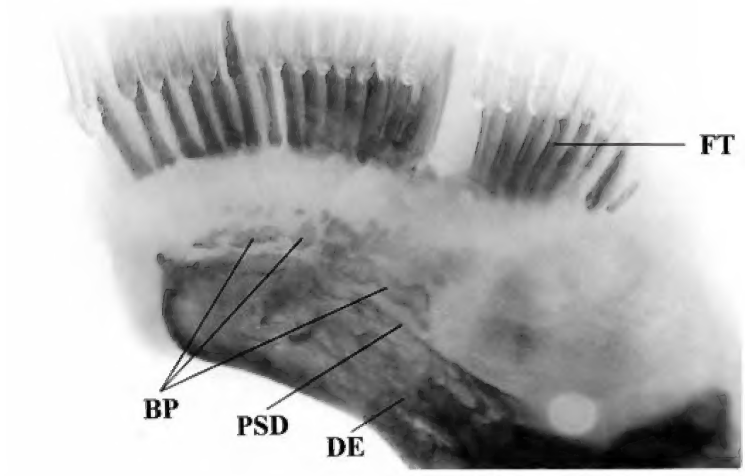
Alticus andersonii (Day, 1876): SB uncat., 1 male, 66.3 mm SL; Indian Ocean, Sri Lanka, Trincomalee.
Blenniella cyanostigma (Bleeker, 1849): SB uncat., 1 male, 50.7 mm SL; Indian Ocean, Sri Lanka, Galle.
Entomacrodus cadenati Springer, 1966: SB uncat., 1 male, 53.2 mm SL; East Atlantic Ocean Senegal, Dakar, Ile de Gorée.
Entomacrodus vermiculatus (Valenciennes in Cuvier & Valenciennes, 1836): SB uncat., 1 female, 84.3 mm SL; Indian Ocean, Sri Lanka, Trincomalee.
Exallias brevis (Kner, 1868): SB uncat., 1 male, 77.8 mm SL; Pacific Ocean, Taiwan, Lanyu; coll. S.-C. LEE.
Istiblennius edentulus (Schneider & Forster in Bloch & Schneider, 1801): SB uncat., 1 male, 83.0 mm SL; *Indian* Ocean, Sri Lanka, Hikkaduwah.
Istiblennius rivulatus (Rüppell, 1830): SB uncat., 1 male, 96.5 mm SL; Red Sea, Gulf of Aqaba, Israel, Eilat.
Nannosalarias nativitatus (Regan, 1909): SB uncat., 1 male, 28.2 mm SL; Indian Ocean, Christmas Island; coll. G.R. ALLEN.
Ophioblennius atlanticus (Valenciennes in Cuvier & Valenciennes, 1836): SB uncat., 1 female, 78.3 mm SL; East Atlantic Ocean, Senegal, Dakar, Ile de Gorée.
Praealticus tanegasimae (Jordan & Starks, 1906): SB uncat., 1 male, 87.6 mm SL; Pacific Ocean, Japan, *Tanega*-shima.
Salarias fasciatus (Bloch, 1786): SB uncat., 1 male, 41.0 mm SL; Indian Ocean, Sri Lanka, Galle.
Salarias sinuosus Snyder, 1908: SB uncat., 1 male, 33.6 mm SL; Indian Ocean, Sri Lanka, Trincomalee.

2.3. Acknowledgement

I would like to thank Dr. R. FRICKE (SMNS, Stuttgart) for supporting the present study.

3. Dentition of Group 4 of the Subfamily Salariinae

Species of Group 4 of the subfamily Salariinae examined in the present study share the following dentition characters: premaxillary and dentary forming a complete shell; anterior-superior margin of both premaxillary and dentary freely, roof-like protruding; bases of functional teeth are widely separated from posterior-inferior margin of premaxillaries and posterior-superior margin of dentaries; posterior-inferior margin of premaxillaries and posterior-superior margin of dentaries are attached with the bases of the functional teeth by a membrane consisting of connective tissue; bony inlays are found within this membrane.



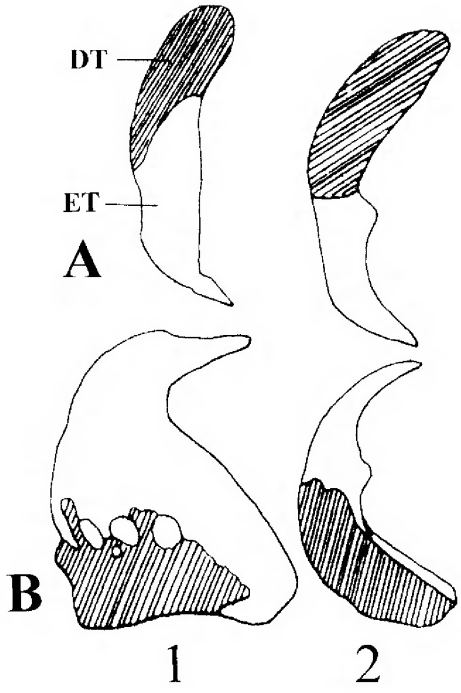
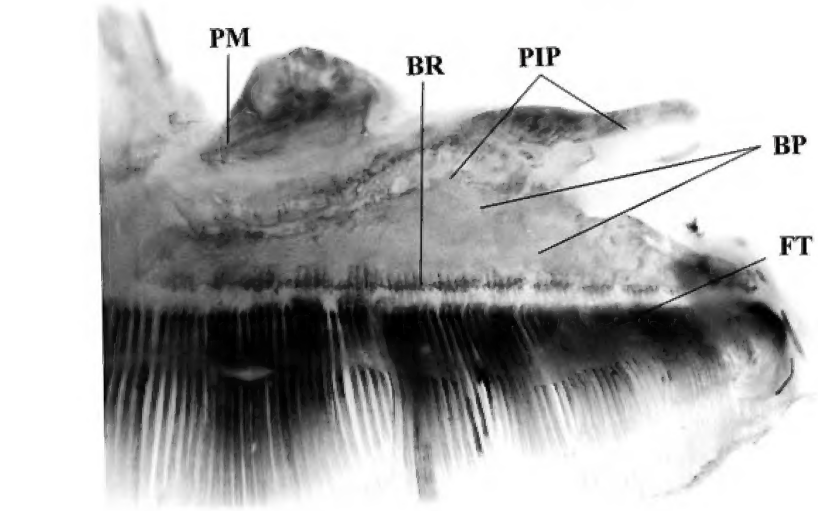


Fig. 1. *Exallias brevis*, male, 77.8 mm SL. – (*Upper*): Right dentary, superior view. Replacement teeth removed.
Fig. 2. Functional teeth in median sections of premaxillary *(A)* and dentary *(B)*. – (*Lower*): 1. *Exallias brevis*; – 2. *Nannosalarias nativitatus*.

However, significant variation is found for the following characters: Distance between the bases of the functional teeth and the jaw margins; density, localisation and configuration of the bony inlays in the connective tissue membrane between the bases of the functional teeth and the posterior margins of the jaw bones. The differences cannot be classified in groups, but need separate descriptions, as some patterns were only found in single species.



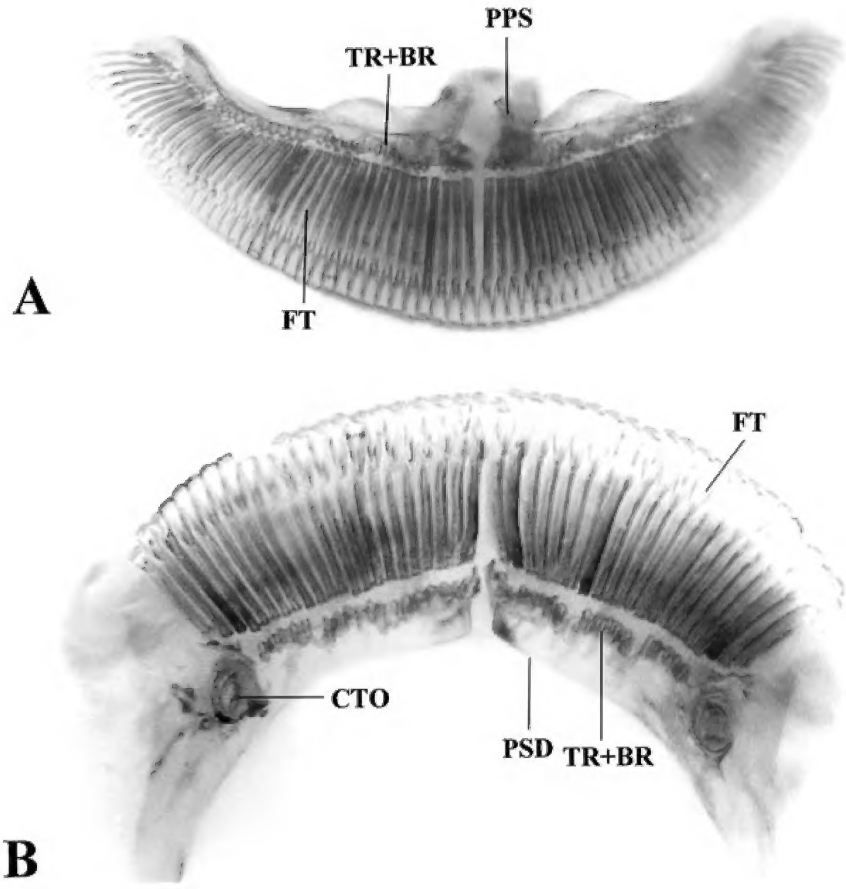
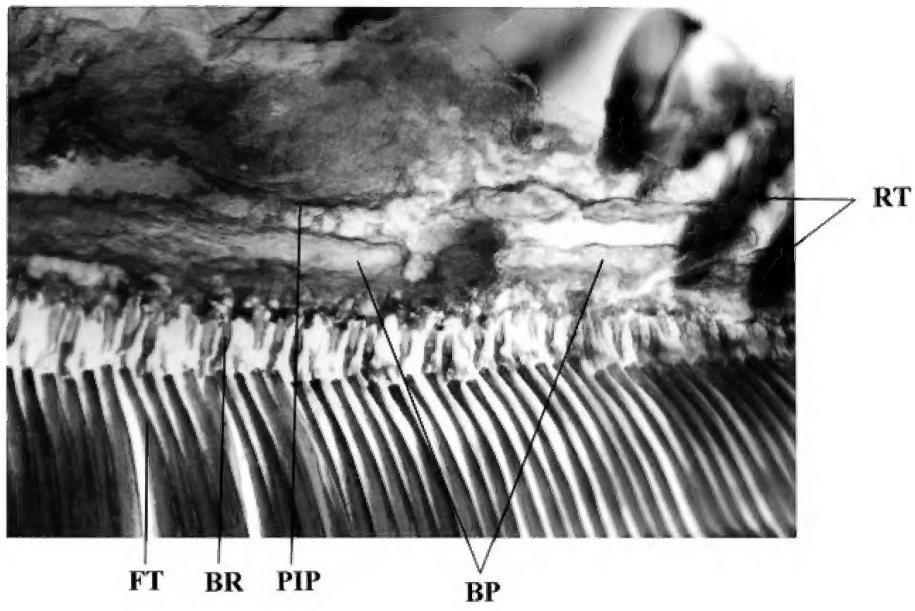


Fig. 3. *Exallias brevis*, male, 77.8 mm SL. – (*Upper*): Right premaxillary, posterior view. Replacement teeth removed.

Fig. 4. *Nannosalarias nativitatus*, male, 28.2 mm SL. – (*Centre*): *A.* Premaxillaries, inferior view; – (*Lower*): *B.* dentaries, superior view.



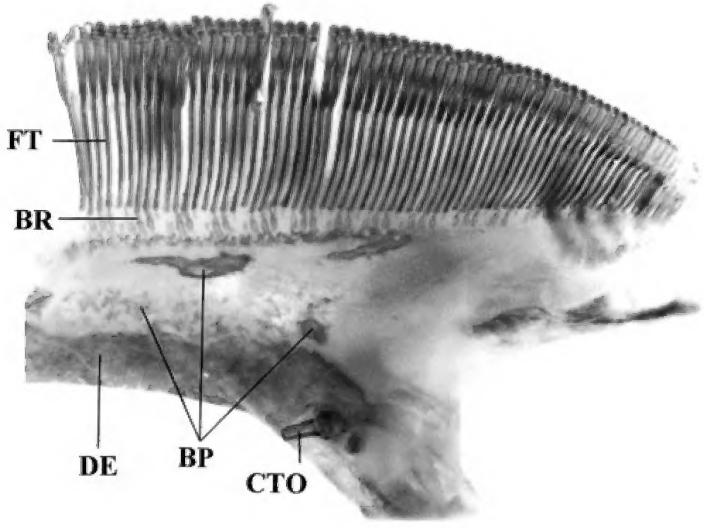


Fig. 5. *Entomacrodus vermiculatus*, female, 84.3 mm SL. – (*Upper*): Right premaxillary, posterior view. Replacement teeth removed.
Fig. 6. *Entomacrodus vermiculatus*, female, 84.3 mm SL. – (*Lower*): Right dentary, superior view. Replacement teeth removed.

In all species of Group 4, rodlet-like bony particles adjacent to the bases of the functional teeth are found. These bony particles are remains of the basal tooth plates which originally connected the functional teeth with the jaw margins.

An exception for this character is found in *Exallias brevis* (Fig. 1). This species has a relatively narrow distance between the bases of the functional teeth and the upper posterior margin of the dentaries. In the membrane connecting the bases of the functional teeth and the posterior margin of the dentaries, irregular configurated bony

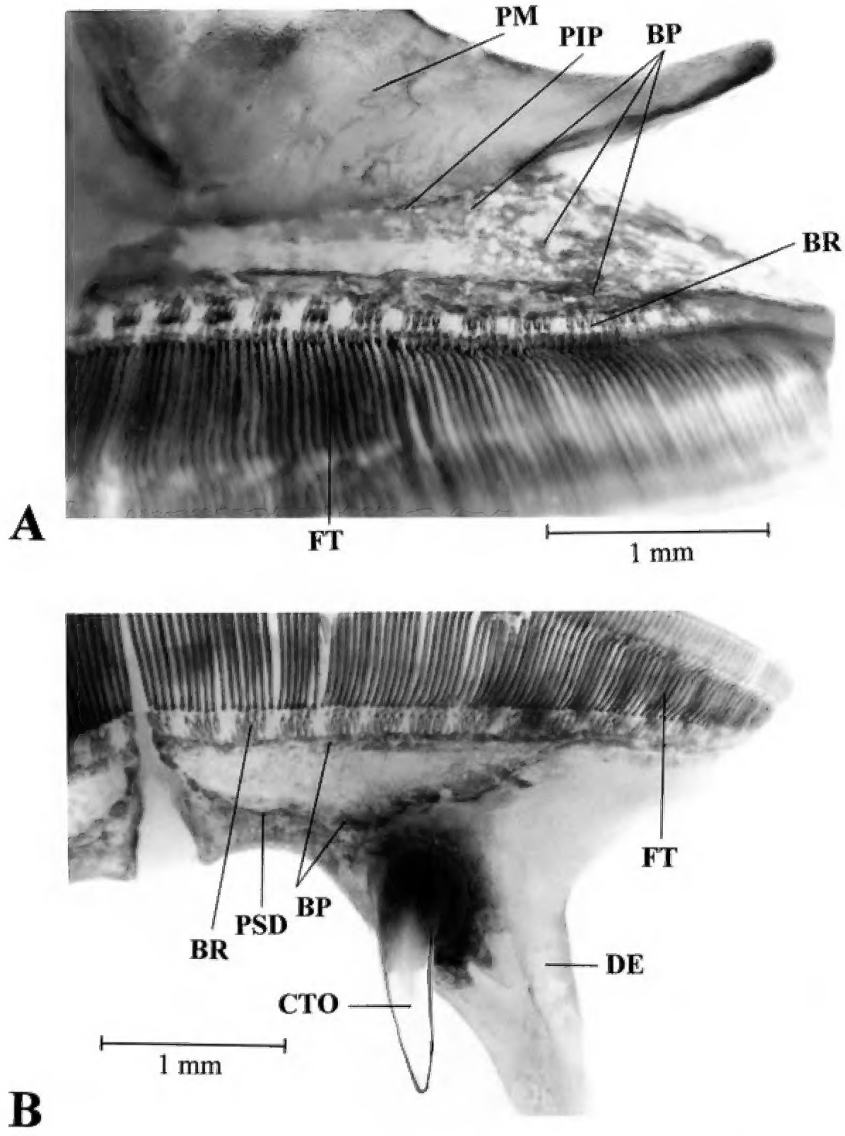


Fig. 7. *Entomacrodus cadenati*, male, 53.2 mm SL. – *A.* Right premaxillary, posterior view. Replacement teeth removed; – *B.* right dentary, superior view. Replacement teeth removed.

particles of varying sizes are found close to the vaguely shaped margin of the dentaries (Fig. 1, BP). Rodlet-shaped bony particles in regular arrangement are found in the premaxillary (Fig. 3 BR), but not in the dentary (Fig. 1).

The premaxillary of *Exallias brevis* has 194–210 comblike, functional teeth. In the membrane connecting the bases of the functional teeth with the posterior margin of the premaxillary, irregularly configurated but mostly large, thin, elongate, adjacent bony inlays are found. In between these bony inlays and the tooth bases, regularly arranged rodlet-like bony inlays are found that are attached to the tooth bases on one side, and to the elongate, adjacent bony inlays on the other side (Fig. 3 BR). The posterior-inferior margin of the premaxillaries is absolutely blurred and has bony connections to the elongate, adjacent bony inlays (Fig. 3).

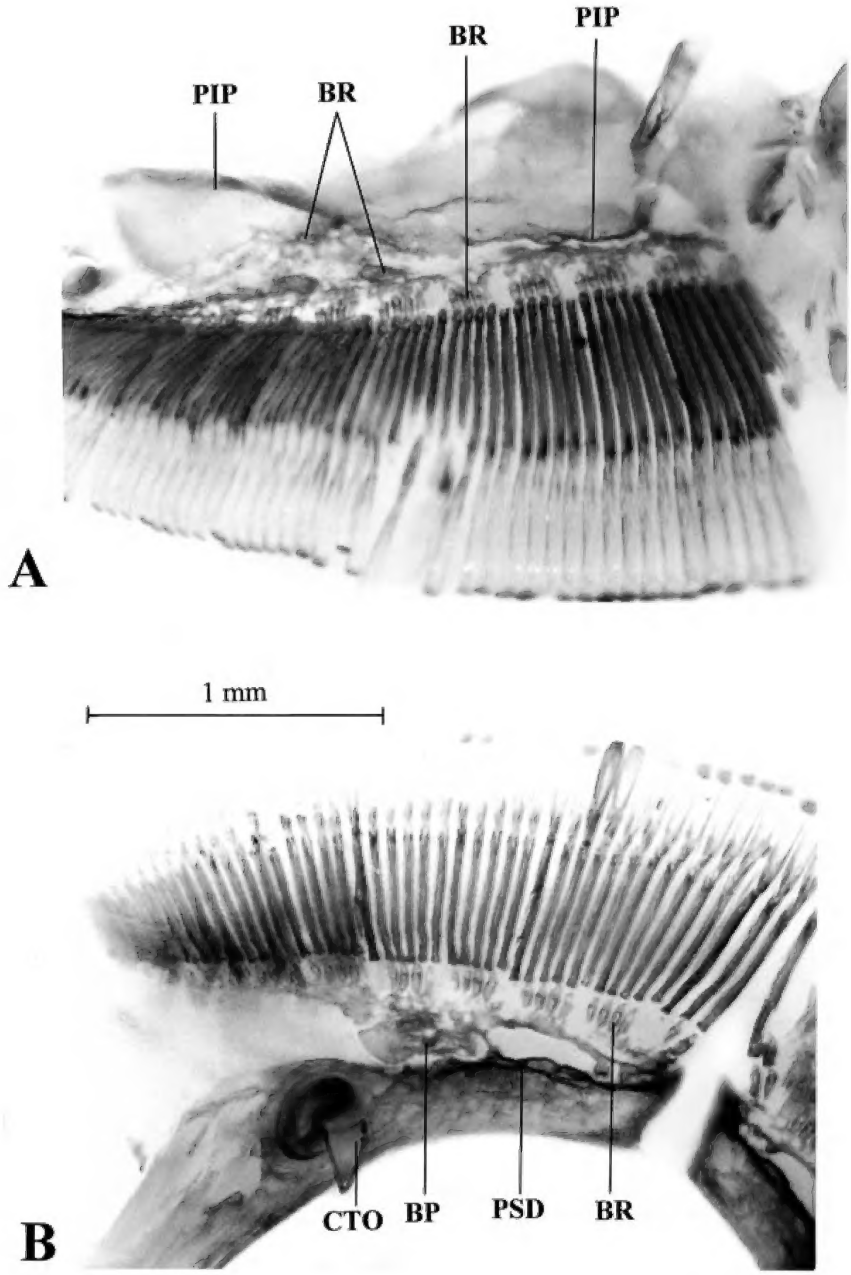


Fig. 8. *Blenniella cyanostigma*, male, 50.7 mm SL. – *A.* Left premaxillary, anterior view. Replacement teeth removed; – *B.* left dentary, superior view. Replacement teeth removed.

Rodlet-like bony inlays in the membrane connecting the bases of the functional teeth and the posterior margins of premaxillary and dentary were found in *Alticus andersonii*, *Blenniella cyanostigma*, *Entomacrodus cadenati*, *E. vermiculatus*, *Istiblennius edentulus*, *Ophioblennius atlanticus*, *Praealticus tanegasimae*, and *Salarias fasciatus*.

In *Entomacrodus vermiculatus*, the rodlet-like bony inlays in the premaxillary and dentary are mostly complete; at their distal end, they are in close contact to the

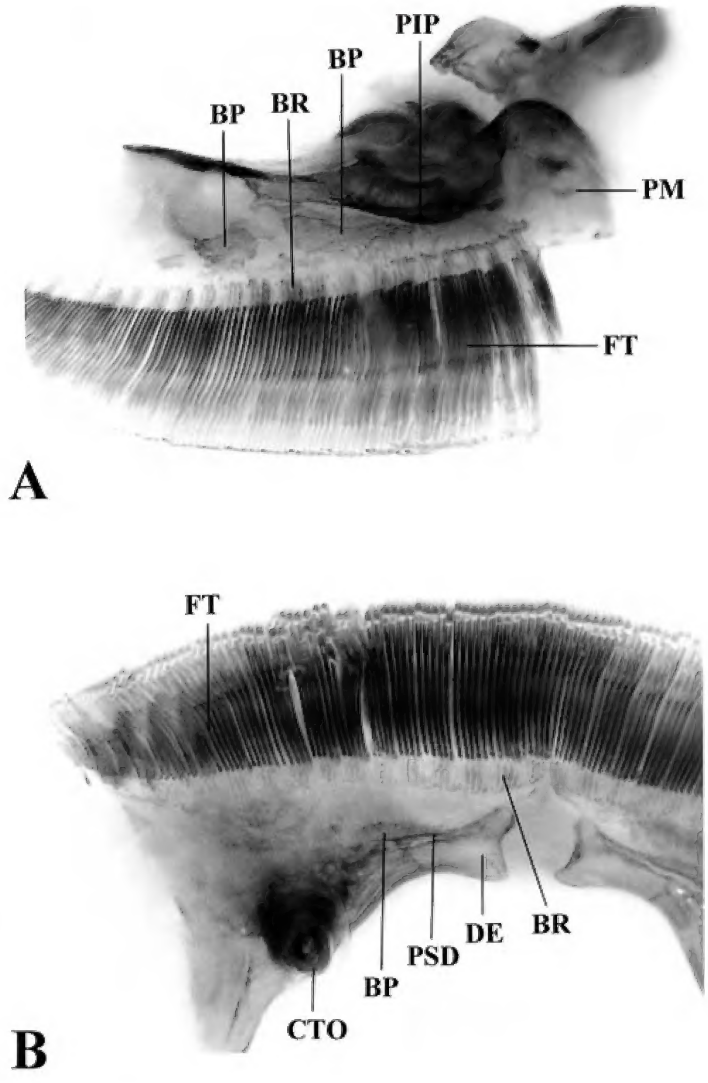


Fig. 9. *Praealticus tanegasimae*, male, 87.6 mm SL. – *A.* Left premaxillary, posterior view. Replacement teeth removed; – *B.* left dentary, superior view. Replacement teeth removed.

tooth bases. In the premaxillary, the proximal end is in contact with irregularly configurated, partially elongate bony particles (Fig. 5 BP). The posterior-inferior margin of the premaxillary has a blurred contour (Fig. 5 PIP). The same situation is found in the dentary of *Entomacrodus vermiculatus* (Fig. 6). In the dorsal membrane, however, significantly less bony particles are found than in the premaxillary. *Entomacrodus cadenati* has less bony particles in the membranes between functional tooth bases and jaw bones (Fig. 7 A-B).

In *Blenniella cyanostigma* (Fig. 8 A-B: BR) and *Praealticus tanegasimae* (Fig. 9 A-B: BR), the rodlet-like bony inlays in both jaws are connected with the bases of the functional teeth and with irregularly configurated bony particles in the membrane towards the posterior margins of premaxillary and dentary. The functional teeth are comb-like, with rounded bases.

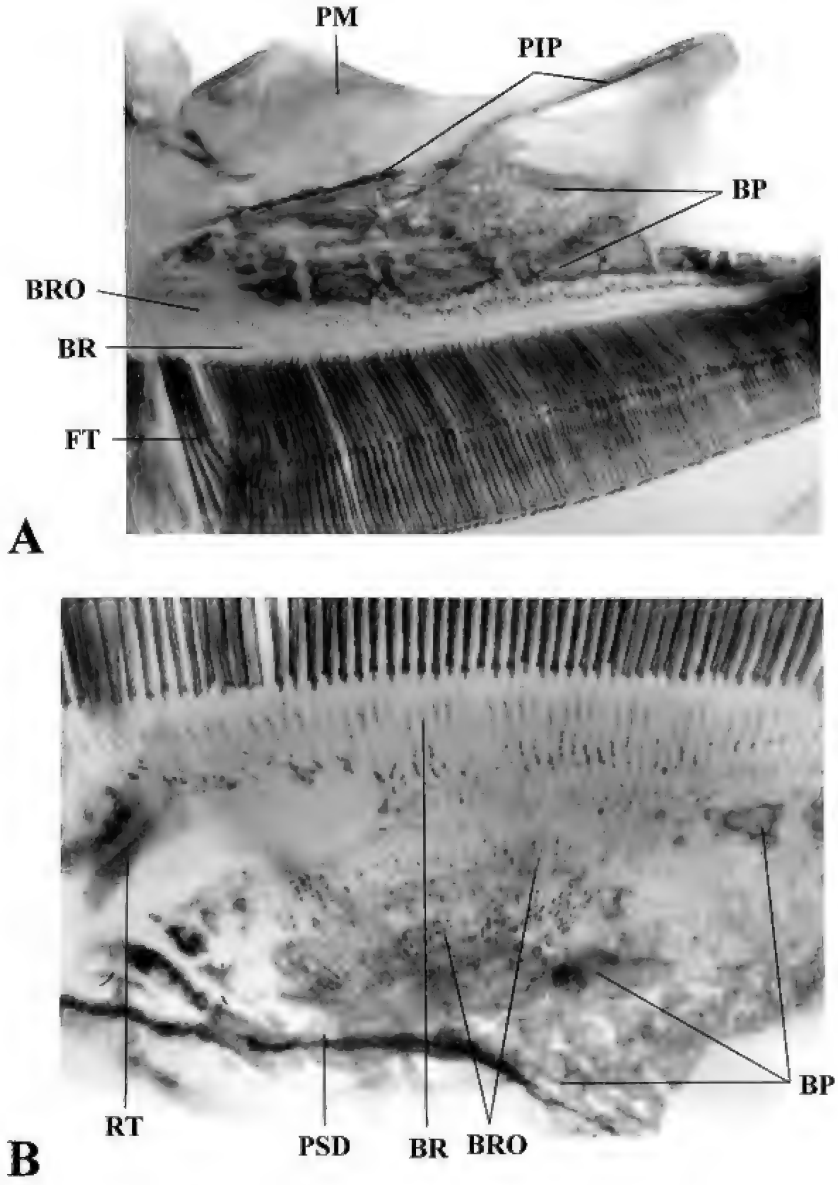
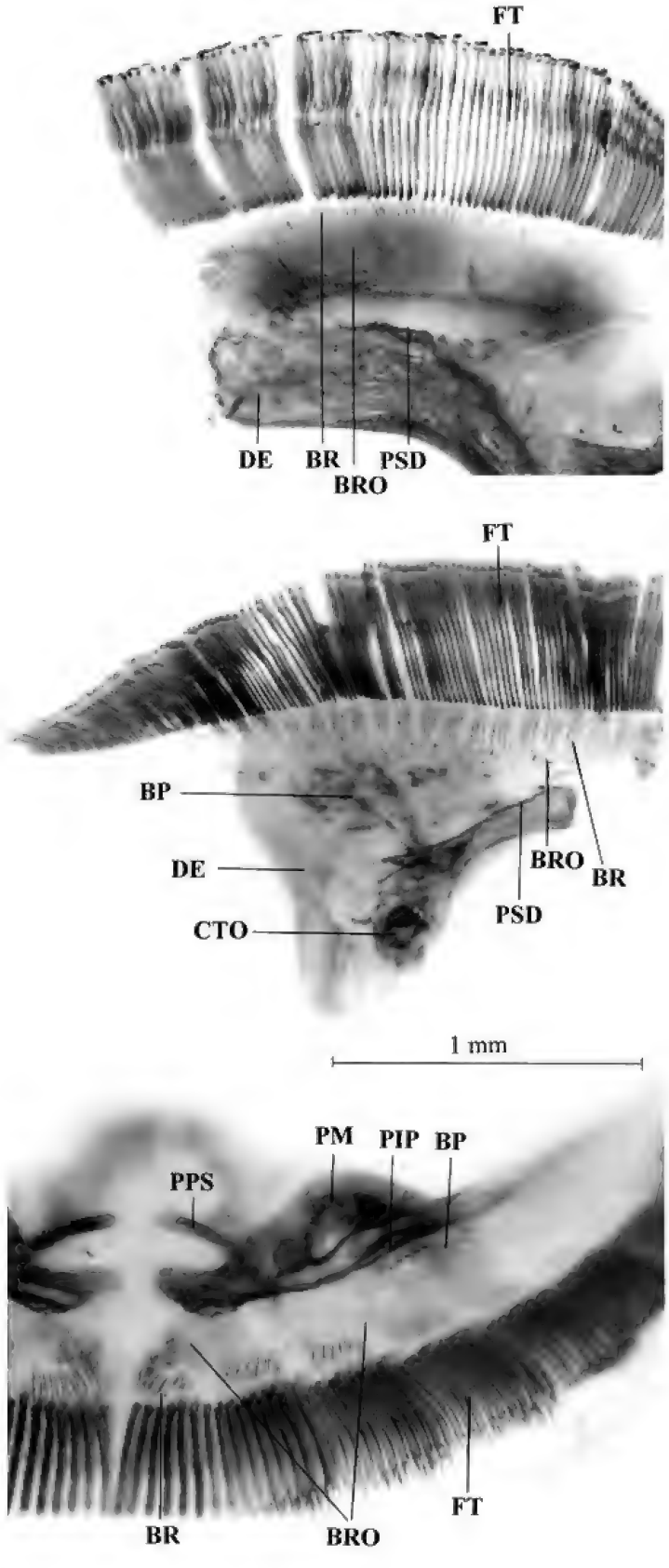


Fig. 10. *Istiblennius edentulus*, female, 74.4 mm SL. – *A.* Right premaxillary, inferior view. Replacement teeth removed; – *B.* right dentary, superior view. Replacement teeth removed.

In *Blenniella cyanostigma*, *Entomacrodus cadenati*, *E. vermiculatus*, and *Praealticus tanegasimae*, the bony particles in the membrane between the bases of the functional teeth and the posterior margins of the premaxillary and dentary are irregularly shaped and of different sizes and configurations. On the other hand, *Istiblennius edentulus* has transverse rows of small bony particles in longitudinal arrangement in the membrane (Fig. 10 A-B: BRO). Some of these bony particles extend in the dentary and, to a lesser degree, in the premaxillary, from the distal end of the rodlet-like bony particles (BR) at the bases of the functional teeth towards the posterior-superior margin of the dentary (Fig. 10 B: PSD). Towards the posterior-inferior margin of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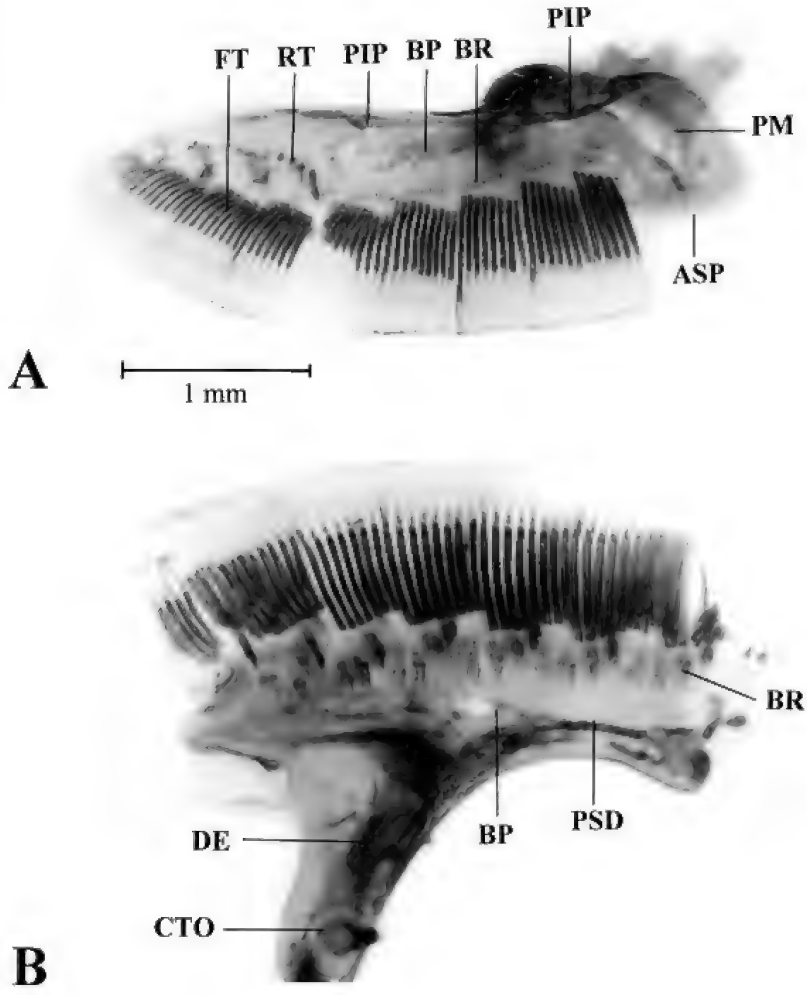

Fig. 14. *Salarias fasciatus*, male, 41.0 mm SL. – *A.* Left premaxillary, posterior view. Median section of replacement teeth removed; – *B.* left dentary, superior view.

the premaxillary, and (to a lesser degree) towards the posterior-inferior margin of the dentary, the transverse rows of bony particles in the membrane are replaced by larger, irregularly configurated and larger, elongate bony particles, as described for *Entomacrodus* spp.

A pattern similar to *Istiblennius edentulus* is found in the species *I. rivulatus* (Fig. 11), *Alticus andersonii* (Fig. 12), and *Salarias sinuosus* (Fig. 13: BRO). In *Salarias fasciatus* (Fig. 14 A-B), however, no transverse rows of bony particles were found in the membrane.

Fig. 11. *Istiblennius rivulatus*, male, 96.5 mm SL. – (*Upper*): Right dentary, superior view. Replacement teeth removed.

Fig. 12. *Alticus andersonii*, male, 66.3 mm SL. – (*Centre*): Left dentary, superior view. Replacement teeth removed.

Fig. 13. *Salarias sinuosus*, male, 33.6 mm SL. – (*Lower*): Right premaxillary, inferior view. Replacement teeth removed.

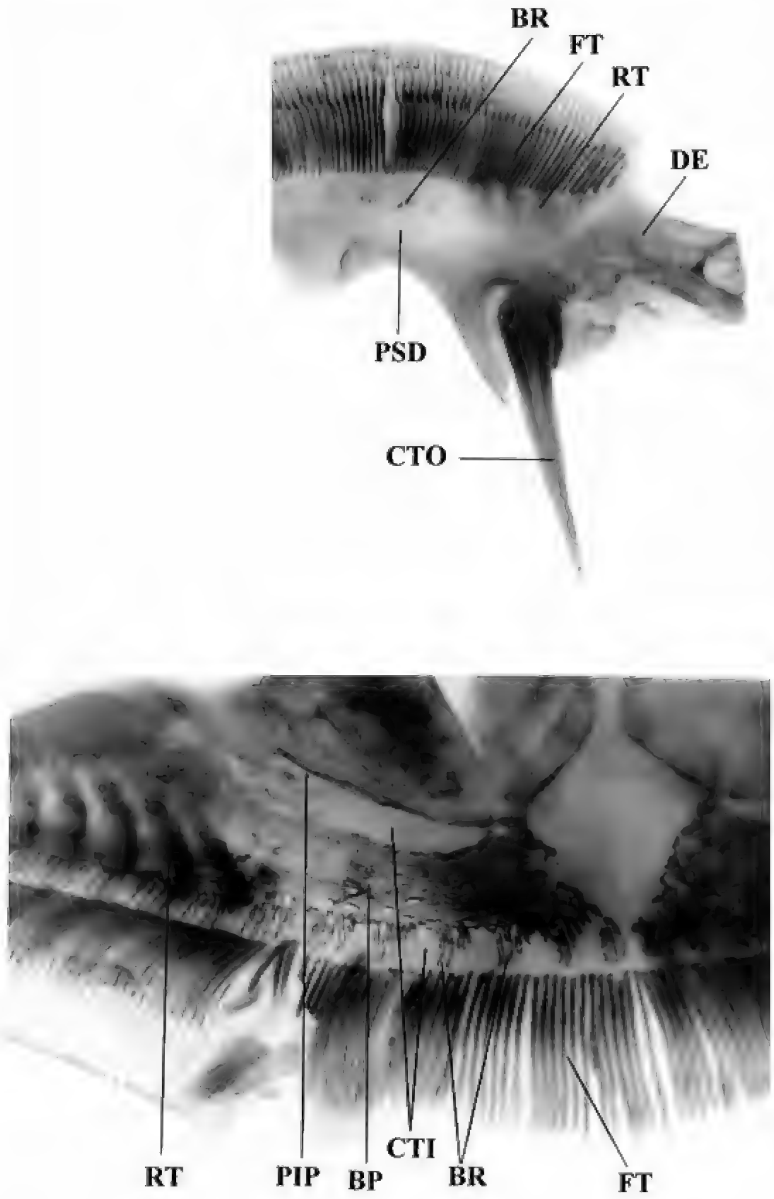

Fig. 15. *Ophioblennius atlanticus*, female, 78.3 mm SL. – (*Upper*): Right dentary, superior view.

Fig. 16. *Ophioblennius atlanticus*, female, 78.3 mm SL. – (*Lower*): Left premaxillary, inferior view. Median section of replacement teeth removed.

Ophioblennius atlanticus has another, different pattern. In the connective tissue membrane between the bases of the functional teeth and the posterior-superior margin of the dentary, rodlet-like bony particles are found. Neither additional rows of bony particles, nor irregularly shaped bony inlays can be found. The posterior-superior margin of the dentary has a clear margin. The caniniform teeth in the dentary are much larger than in other species of Group 4 of the Salariinae examined in the present study (Fig. 15). In the membrane connecting the bases of the functional teeth with the posterior-inferior margin of the premaxillary, broad, elongate, adjacent bony inlays are found which are connected with the rodlet-like bony particles.

4. Discussion

The characters of dentition observed in *Exallias brevis* give an important hint about the evolution of the dentition of Group 4. The lack of rodlet-like bony particles is obviously related to the typical configuration of the lower jaw incisors (Fig. 2, B1), and to their low number of 52–62 which is typical for an incisiviform pattern. It suggests that the basal plates have not yet separated from the tooth bases. Rodlet-like particles are only found in species with a comblike dentition; incisors are situated directly on the bony jaw plates, with no intermediate bony particles.

The rodlet-like bony inlays in the membrane between the bases of the functional teeth and the posterior margin of the premaxillary originate from the former basal tooth plates.

Anatomical characters of species of the subfamily Salariinae that show an evolutionary trend to form a comblike dentition are first found in the premaxillary. If the premaxillary already forms a bony shell with a free anterior-superior margin and typical comb-like teeth, the teeth in the dentary may still have an incisiviform pattern (BATH, 2001).

The evolution of rodlet-like bony inlays out of basal tooth plates is clearly visible in the dentition patterns of species of Group 3 (BATH, 2001). In these species, the bases of the functional teeth have gradually been separated from the basal plates of the former tooth ridge (e.g. *Nannosalarias nativitatus*, Fig. 4 A, B: TR, BR). Rodlet-like bony inlays in most species of Group 4 are considered as remains of the former basal tooth plates.

Istiblennius edentulus has series of bony particles in a transverse arrangement within the membrane connecting the bases of the functional teeth with the posterior margins of the jaw bones. Like the rodlet-like bony inlays, these bony particles originate from the former basal plates of the functional teeth. This is demonstrated by the number of bone rows that equals the number of rodlet-like bony particles and the number of functional teeth (Fig. 10 B: BRO).

Ophioblennius atlanticus has rodlet-like bony particles in the dentary membrane, but lacks additional bony particles. This may be explained by the extraordinary size of the caniniform teeth. Caniniform teeth, which are in direct contact with the jaw bones, are much better attached to the jaws and more stable than the flexible teeth that are not in direct contact. The additional bony particles in the premaxillary membrane are comparable with the premaxillary of *Entomacrodus vermiculatus* (Fig. 16).

The functional significance of the bony particles in the membrane between the bases of the functional teeth and the posterior margins of the jaw bones may be a bony support of the functional teeth. The number of bony particles in the dentary membrane is not significantly correlated with the presence or size of caniniform teeth.

Summarising the observations, it seems evident that bony particles in Group 4 are faster reduced in the dentary membrane than in the premaxillary membrane. A reason may be the originally more stable situation of the dentary with its joint connection between articular and quadrate towards the viscerocranium. On the other hand, the premaxillary is attached to the maxillary, the palatine and to the median ethmoid (with the processus acscendens) by connective tissue only.

5. References

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